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The Journal of HEREDITY

A monthly publication devoted to Plant Breeding Animal Breeding and Eugenics

DECEMBER, 1924

HAIRLESS MICE
F. B. SUMNER

COURTSHIP OF THE CALOBATAS
WILLIAM MORTON WHEELER

FREQUENCY OF MUTATIONS IN MAIZE
HAYES AND BREWBAKER

HEREDITARY CROOKED FINGERS
R. A. HEFNER

TITLE PAGE AND INDEX—VOLUME XV

PUBLISHED BY THE
AMERICAN·GENETIC·ASSOCIATION
BALTIMORE, MD. AND WASHINGTON, D.C.

Volume XV Number 12

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The

Journal of Heredity

VOL. XV, NO. 12 DECEMBER, 1924

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The JOURNAL OF HEREDITY is published monthly by the

AMERICAN GENETIC ASSOCIATION

At 1918-32 Harford Avenue, Baltimore, Md., and

Victor Building, Washington, D. C.

Address communications regarding editorial matters and the business management of the Association to Room 306, Victor Building, Washington, D. C.

Entered as second class matter February 24, 1923, at the post office at Baltimore, Maryland. Acceptance for mailing at the special rate of postage provided for in Section 1103, Act of October 3, 1917, authorized December 20, 1918. Contents copyrighted 1924 by the American Genetic Association. Reproduction of articles or parts of articles permitted only upon request, for a proper purpose, and provided due credit is given to the author and to the JOURNAL OF HEREDITY, Washington, D. C.

Date of Issue of This Number, January 25, 1925

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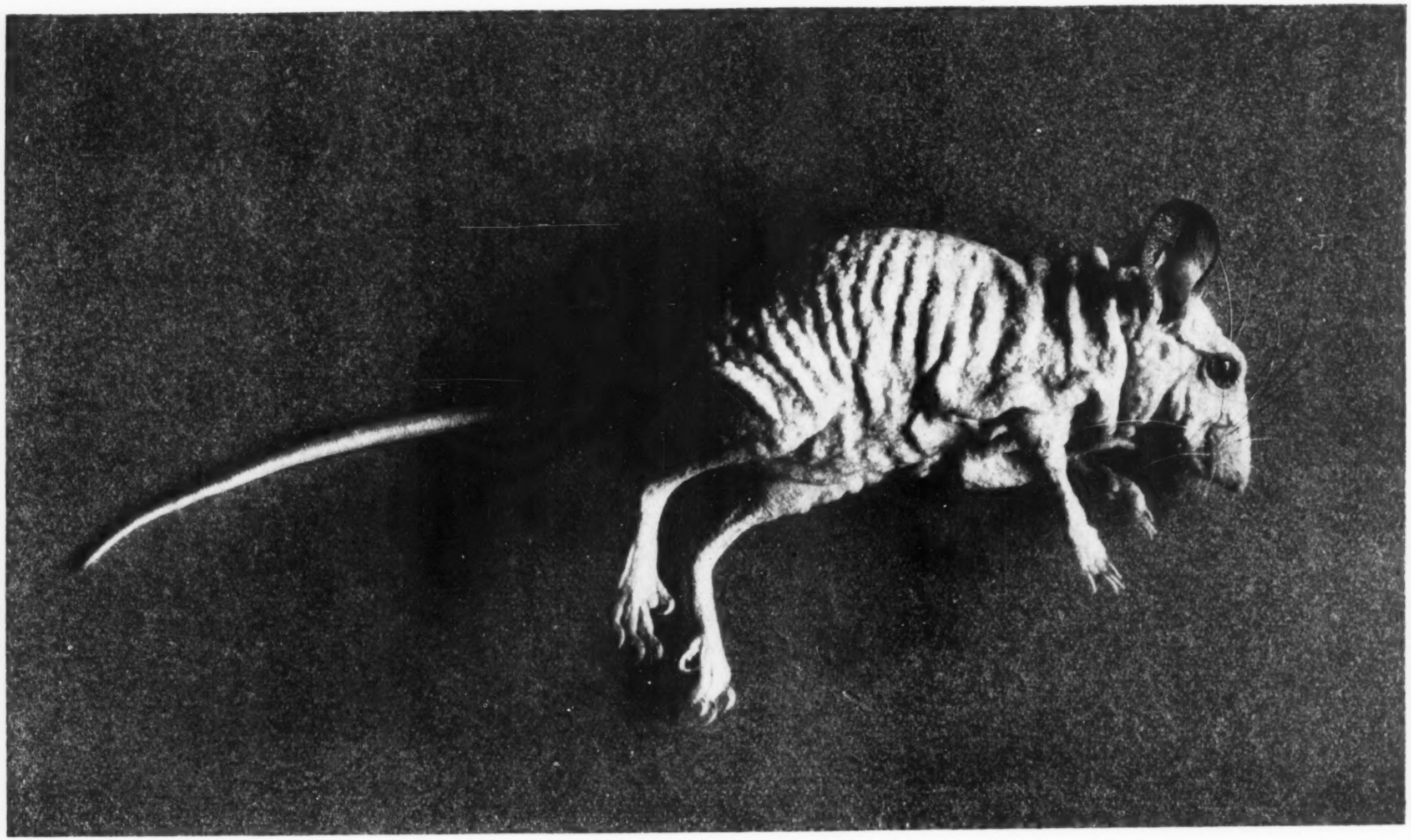


A RHINOCEROS MOUSE

Frontispiece

Hairless Peromyscus result from a recessive mutation of rare occurrence. These mice acquire the juvenile coat of hair, which begins to fall out at the age of about two weeks. Depilation is usually practically complete within a few weeks more, though scattered hairs may persist for some time, as shown in Figures 1 and 2. The vibrissæ always remain normal. Note the exceptional development of folds of the skin and elongation of the claws. The corrugated skin has suggested the name "Rhinoceros Micæ." These folds sometimes become so deep as to render the animals blind. The mouse is 6½ months old. Photograph by T. L. Miller

HAIRLESS MICE

F. B. SUMNER

Scripps Institution, La Jolla, California

HAIRLESS rats and mice have been reported by Gordon,[1] Gaskoin,[2] Bree,[3] Marshall,[4] Bateson,[5] Beddard,[6] Allen,[7] Belcher,[8] Pocock,[9] Millais,[10] Campbell,[11] Friedenthal,[12] Barrett-Hamilton and Hinton,[13] and by the Year-Book of the Amateur Menagerie Club.[14] Doubtless other references occur in zoological literature, but an exhaustive search has seemed hardly warranted.* Figures of this abnormality have been published by Gaskoin, Allen, Belcher, Campbell and Friedenthal. The animals observed by the foregoing writers appear to have been exclusively house-mice and house-rats (*Mus mus-culus* and *Epimys norvegicus*).

Dr. Oscar Riddle has kindly furnished me two specimens of hairless *Mus musculus* which were caught in one of the pigeon buildings of the Station for Experimental Evolution at Cold Spring Harbor, New York. A number of these animals, he informs me, were captured or seen in this same building during the years 1915 and 1916. Some excellent photographs were obtained by Dr. A. M. Banta of the station staff.

From the various published descriptions, it is not entirely certain whether the writers here cited have all been dealing with identical mutations. Most of the descriptions include reference to conspicuous corrugations of the skin, a condition which has suggested the name "rhinoceros mice." Gaskoin proposed the varietal name *nudoplicatus* for this sport. In Campbell's older specimens, the folds on the head developed to such a degree as to cover the eyes and render the animals blind.

Allen, Campbell, and the writer of the article in the Year-Book of the Amateur Menagerie Club state that the young animals develop the first coat of hair and subsequently lose it. Some others who have reported partially hairless mice may have seen transitional stages in the ontogeny of this character (see below).

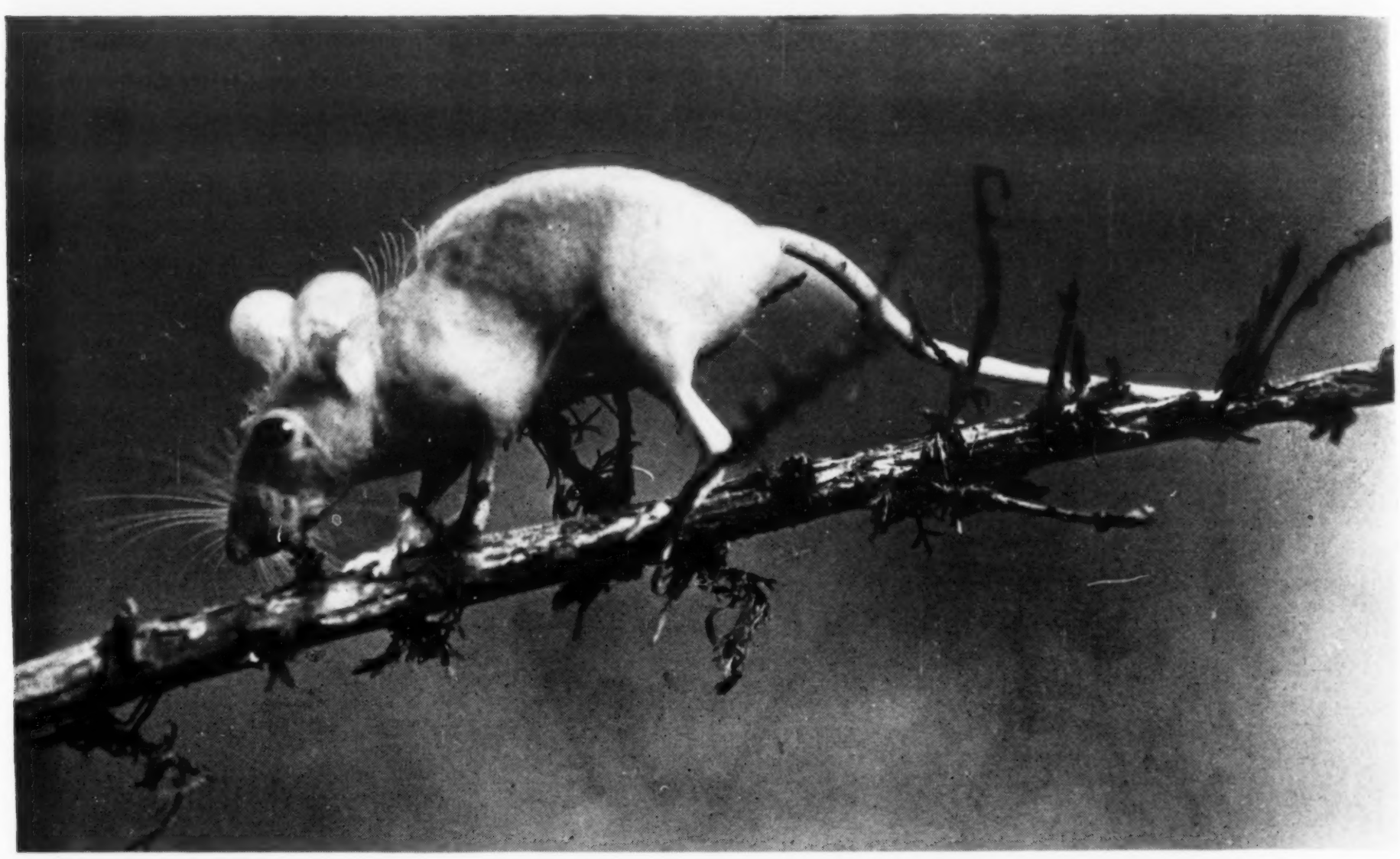
By several the hairless character has been reported to be hereditary. Either two consecutive generations of hairless animals were observed, or several members of a litter displayed this abnormality. Allen's slight success in attempting to raise these mice led him to regard the condition as "pathological," though he thought that it might none the less be hereditary. Campbell's twenty-seven specimens were short-lived and reached the maximum age of 5½ months. Other writers have reported the early death of their specimens.

The hairless character has appeared in our *Peromyscus* stock at La Jolla, on two independent occasions. Since we have reared several thousand broods, derived from several hundred wild ancestors, and have practiced inbreeding extensively in this stock, it is evident that the mutation is of infrequent occurrence, and that heterozygotes are rare in nature.

History of the Hairless Strains

The first hairless specimens of *Peromyscus* appeared in a series of *P. maniculatus gambeli*, reared by Dr. H. H. Collins and myself in 1918. A normal wild female, mated to her cage-bred son (likewise normal), gave birth to four offspring, among which were two females which became hairless. One of these proved to be fertile, to the extent of producing two young when mated to her father.

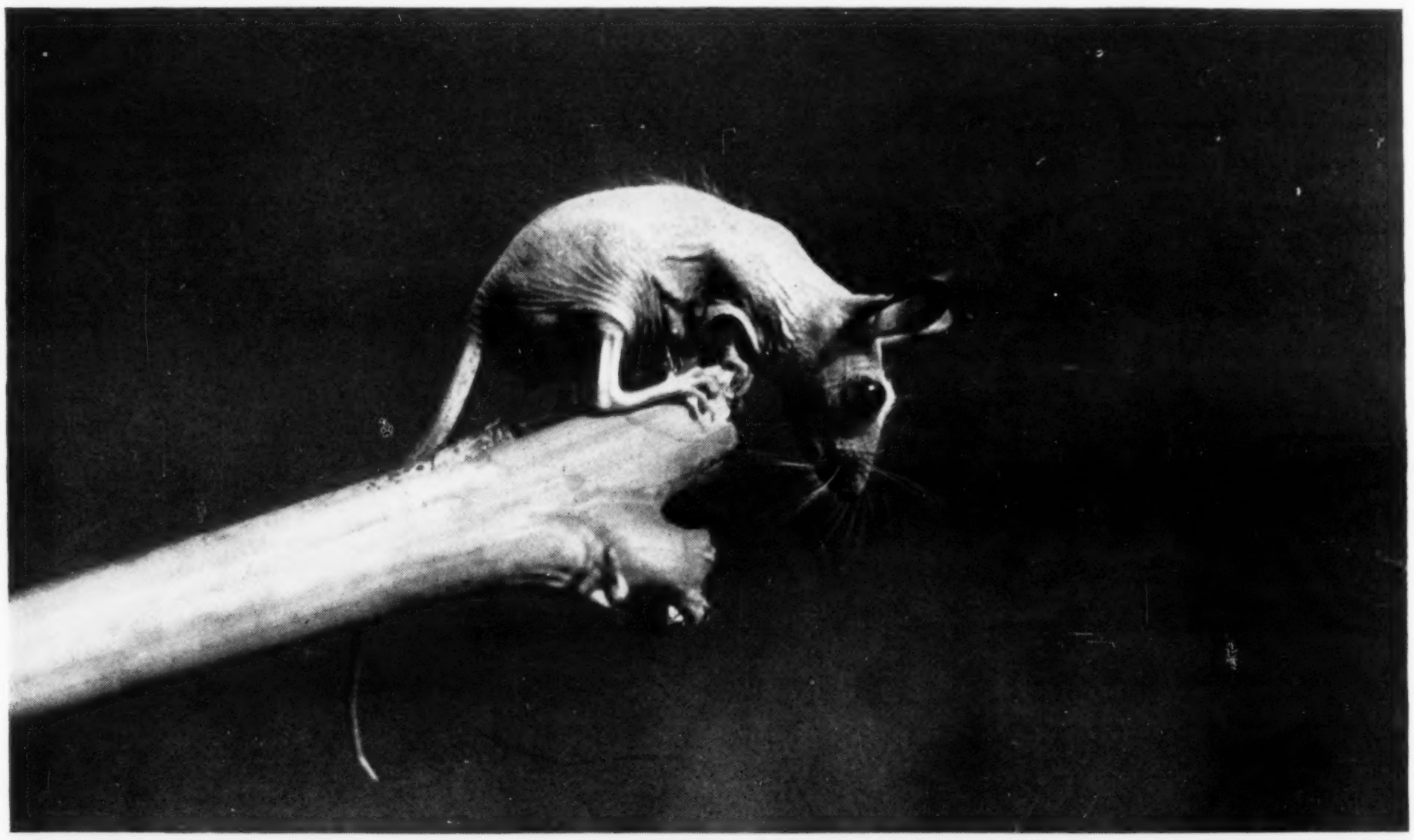
*For several of these references I am indebted to Drs. A. L. and A. C. Hagedoorn.



A YOUNG HAIRLESS ALBINO

Figure 1

There appears to be no linkage between the two recessive characters, hairlessness and albinism. Photograph by H. H. Cleaves.



A YOUNG PIGMENTED HAIRLESS MOUSE

Figure 2

Note the patches of hair, vestiges of the juvenile coat that begins to be shed about the end of the second week. Later on, transitory tufts of hair, or even a fairly complete coat reappears, but soon is shed again. Photograph by H. H. Cleaves.

This circumstance deserves mention, in view of the almost uniform sterility of the hairless females of my second series. Both members of the foregoing brood had normal pelages, and no other young were obtained.

The second appearance of "hairless" in my *Peromyscus* stock occurred in 1921, among the offspring of two F_1 hybrids (these being sibs), resulting from a cross between albino and yellow mutants. Since both of these mutant strains arose among pure *gambeli* stock, the second hairless series, like the first, is a derivative of this subspecies. So far as known, the two series are entirely unrelated. At least, the two descent lines contain no individuals in common, commencing with the wild ancestors. Whether or not the mutation occurred *de novo* in our laboratory stock, we have no means of knowing. The first hairless individuals of this series were only four generations removed from certain of their wild ancestors, and one of these may well have been heterozygous.

The pair of hybrids just referred to produced four broods, comprizing eleven young. Of these, four were hairless, seven being normal. In all, fifty-two hairless mice have thus far appeared among the offspring and descendants of this pair. Before discussing the breeding records of these mice, it is desirable to give a brief description of hairless *Peromyscus*, along with some mention of their life history.

Description of the Hairless Mice

Up to the age of about two weeks, the potentially hairless individuals are indistinguishable from ordinary ones. A normal juvenile pelage is acquired, which appears to be of average density. The loss of the hair commonly commences at the age of two to three weeks, and requires several weeks or even months for its completion. Most frequently a thinning is first observed on the dorsal surface of the head, which may be accompanied or preceded by the appearance of a bare area on the snout. This thinning of the hair spreads rapidly to the trunk region and large areas soon become completely naked.* There is, however, much variation in the course of the depilatory process, as well as in its duration. Local patches of fine hair may remain for weeks or even for many months after the remainder of the coat has disappeared (Figures 1 and 2). A curious phenomenon is the reappearance of transitory tufts of hair, or even of a large part of the pelage, after the body has completely lost the original coat. This, however, soon disappears again. These transitory hairs are largely lacking in pigment and may be nearly white.

None of these mice are strictly "hairless," for all possess a full equipment of vibrissae, as well as of superciliary bristles. In some cases, too, close inspection may likewise reveal the presence of widely scattered single hairs on almost any part of the body.

Two further characters of general occurrence among these mutants are the overdevelopment of the claws, and the corrugated condition of the skin. It is curious to find this hypertrophy of skin structures, in association with an almost complete atrophy of the pelage. So far as examined, hairless mice possess perfectly normal teeth, contrasting, in this respect, with some hairless animals which have been described.

The claws are commonly noticeably elongated, this being particularly true of those belonging to the hind foot. In extreme cases, they may be grotesquely curved, that of the hallux, in particular, being drawn out into a spiral (Frontispiece). Two of Campbell's photographs indicate that the claws of some of h ianimals were likewise greatly exaggerated.

*According to Campbell loss of hair in *Mus* "begins about the eyes and on the belly." Early depilation may, in some cases, have occurred on the ventral surface of *Peromyscus*, and been overlooked by me.

The corrugation of the skin is not nearly as constant a feature of hairless *Peromyscus* as are the hypertrophied claws. The condition is not manifested at all until the animal is several months old, and it may not be pronounced at any age. In my stock, it has never reached such an extreme stage as appears to be common in *Mus musculus* (cf. Campbell's figures). The skin folds occupy various positions on the body. Extensive lateral folds may connect the bases of the fore and hind limbs, suggesting the volplaning membranes of the flying squirrel. Enormous creases may encircle the region of the neck and shoulders, while much contorted transverse corrugations decorate the ventral surface of the body (Frontispiece). In many cases, even where few wrinkles are present, the skin is spotted by small pimples or wart-like excrescences, giving it a decidedly pathological appearance.

Most persons are impressed by the great apparent length of the ears in these mice, but this appearance is delusive, and due entirely to the absence of the hair which normally conceals the bases of these appendages. Measurements of more than twenty hairless mice showed that the ears of these individuals were actually somewhat shorter than those of normal *gambeli* of the same body length.

Pigment Pattern of the Ears

A feature of considerable significance in relation to the ears of these mice is the distribution of pigment. Normal specimens of *Peromyscus* have external ears which are more or less heavily pigmented in the regions which are not covered by the fur. Areas which themselves bear fur, or which are concealed by that of the adjacent regions of the head are uncolored.* Now it is of some interest to note that the same distribution of pigment holds in the case of the hairless mice. Those areas of the ears are white which would be covered by hair if hair were present.

This last circumstance makes it seem probable that the pigment pattern of the ears of *Peromyscus* is hereditary, and is quite independent of the incidence of environmental factors (light or temperature) during individual development. For it appears unlikely that the concealment of the basal portions of the ears during the first few weeks after birth would determine the absence of pigmentation throughout the remainder of life. Is not, perhaps, this distribution of pigment dependent upon previous racial history? In the case of nocturnal animals, it is questionable whether light can exert any considerable direct influence upon pigmentation. There is evidence, however, that temperature may have a visible effect, under certain conditions. Schultz[15] found that local exposure of the skin of Himalayan rabbits to reduced temperature, through the removal of hair, led to the production of dark areas on an otherwise white pelage. In *Peromyscus*, Collins[16] observed that experimental removal of hair was followed pretty promptly by the pigmentation of the depilated area, this, in turn, being followed by the replacement of the hair removed.

Is this relation between exposure and pigment distribution in the ears of *Peromyscus* an accidental one, or is it due to the accumulated effects of environmental stimuli, acting through many generations? The present instance belongs to a large class of cases for which the Lamarckian explanation would seem to be the simplest one, whatever else one may think on the subject. All such circumstantial evidence is, of course, quite inconclusive. But so, for that matter, are the negative results of the few brief experiments now on record, dealing directly with the "inheritance of acquired characters."

*The external surface is here referred to. Considerable areas within the ears are unpigmented.

Vitality of the Hairless Mice

Like so many other "mutant" types, hairless *Peromyscus* are animals of enfeebled constitution. They are, for the most part, undersized, and they display a high percentage of sterility. A number of fairly fertile males have been found, to be sure, but only a single female has thus far borne young, among the twenty of this sex, belonging to the second hairless series.* This is true, despite the fact that a large majority have been mated with males of known fertility. That the sterility of these individuals is not a common property of the strain from which they were derived is shown by the fact that many of the heterozygous females have been normally fertile.

Another indication of the reduced vitality of the hairless specimens is to be seen in the deficient number of pure recessives resulting from the matings of heterozygous animals (see below). No such brief span of life has been observed in *Peromyscus*, however, as Campbell has recorded for his hairless *Mus*. At the date of writing, five individuals have reached the age of a year, one being sixteen months old. Since most of the stock has been born within the past year, it is too early to report upon their longevity in general.

Smith[17] and Hart and Steenbock[18] have described a hairless condition among young pigs, which seems to be due to defective endocrine functioning on the part of the mother. Such pigs were either born dead or died shortly after birth. These investigators found independently that the thyroid gland of the mother sow was abnormal, and that the trouble was rectified by administering small doses of potassium iodide with the food, for some time before the birth of the litter.

This seemed a possible clue to the etiology of hairlessness in mice, a supposition in no way inconsistent with the known fact that the latter condition is hereditary. Accordingly, a solution of potassium iodide was added to the mush which constitutes one ingredient of our ration. Six drops of a 0.2% solution per mouse per day, were administered at first; later a 0.4% solution was used. The dosages in these cases (figured as percentages of body weight) were about five and ten times, respectively, those employed by Smith.† Not the slightest effect was observed, although the parents of fifteen hairless mice were subjected to this treatment, for periods varying from three to nine weeks before the birth of the broods, while the latter and some other hairless young were further treated for the first month or more of their lives.

Breeding Results

Despite the sterility of most of the females, fair numbers of hairless mice have resulted, both from mating heterozygous females with hairless males, and from mating heterozygotes *inter se*. The ratios obtained deserve some mention, though the series are not large enough to allow of satisfactory statistical treatment.

Matings in which both parents were heterozygous yielded 101 normal and 28 hairless young. The departure from the numbers expected for a mendelian recessive (96.75 and 32.25) cannot be regarded as significant, though this deficiency in respect to hairless individuals agrees with the next results to be considered.

Matings of heterozygous females with hairless males yielded 34 normal and 21 hairless. This is perhaps a significant departure from the expected 50:50 ratio. These figures, together with those in the preceding paragraph, are such as would result from a lower

*This female bore two broods, one of which died within a few days, the other, consisting of three hairless individuals, has survived. No further conceptions have ensued, though the mother has been remated for several months. It should be added, however, that sterility is not an uncommon result of captivity in otherwise normal *Peromyscus*.

†Assuming that all of the mush was eaten. It is probably safe to say that, on the average, half of it was consumed.

viability of the "hairless" embryos *in utero*. Further evidence in the same direction is derived from a consideration of the size of broods.

Of the 42 broods considered above, 29 contained one or more hairless individuals, while 13 contained none. The mean size of the former broods was 4.0, that of the latter 3.2. While the numbers here available are of course inadequate, the relations are such as would have arisen on the assumption that some of the broods of the latter class were depleted by the death of "hairless" zygotes *in utero*.

The only surviving brood derived from the mating of two hairless parents contained, as already stated, three hairless individuals.

The hairless strain chiefly considered in this paper arose, as mentioned earlier, from a cross between yellow and albino color varieties of *P. maniculatus gambeli*. From the outset, both pigmented and albinic individuals were found among the hairless ones (figures 1 and 2). It was a matter of interest to determine whether any marked linkage exists between hairlessness and the "color" factor. For the purpose of answering this question, double recessives (albino hairless) were mated with mice which were heterozygous for both factors. The distribution of offspring is as follows:

	Hairy	Hairless
Pigmented	12	10
Albino	18	9
	30	19

The great excess of hairy individuals has already been commented upon. This obviously has nothing to do with linkage. The figures, so far as they go, furnish no evidence for linkage between the hairless condition and albinism.

Somewhat larger numbers are available for matings in which both parents were doubly heterozygous, and in which the hairless grandparent, in each case, was an albino.

	Hairy	Hairless
Pigmented	38	11
Albino	9	4
	47	15

It is plain that if linkage occurs between these factors, larger numbers will be required, in order to reveal its presence. The distribution of these classes according to sex likewise gives no reason to suspect the existence of sex linkage.

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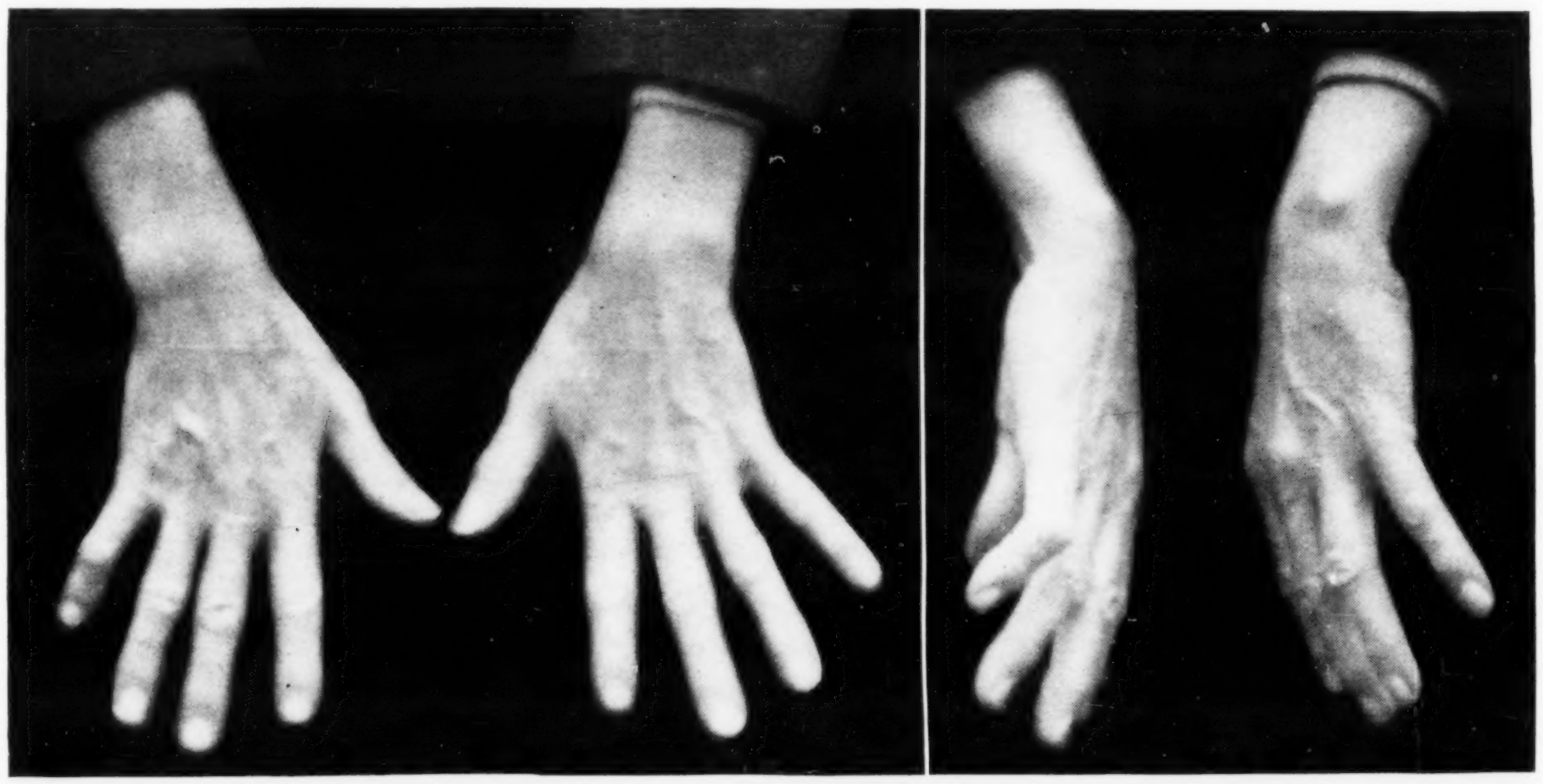
INHERITED ABNORMALITIES OF THE FINGERS

III. Subterminal Articulation in the Proximal Joint of the Little Finger

R. A. Hefner
Ohio State University



ONE FINGER AFFECTED
Figure 3

The little finger of the right hand cannot be straightened, apparently because of the shortness of the tendons having their insertion in the region of the affected joint. The son of this man had both fingers affected, as is shown in the succeeding illustrations.

THIS unusual variation was recently observed in the hands of a fellow student to whom the credit for the collection of data is due.

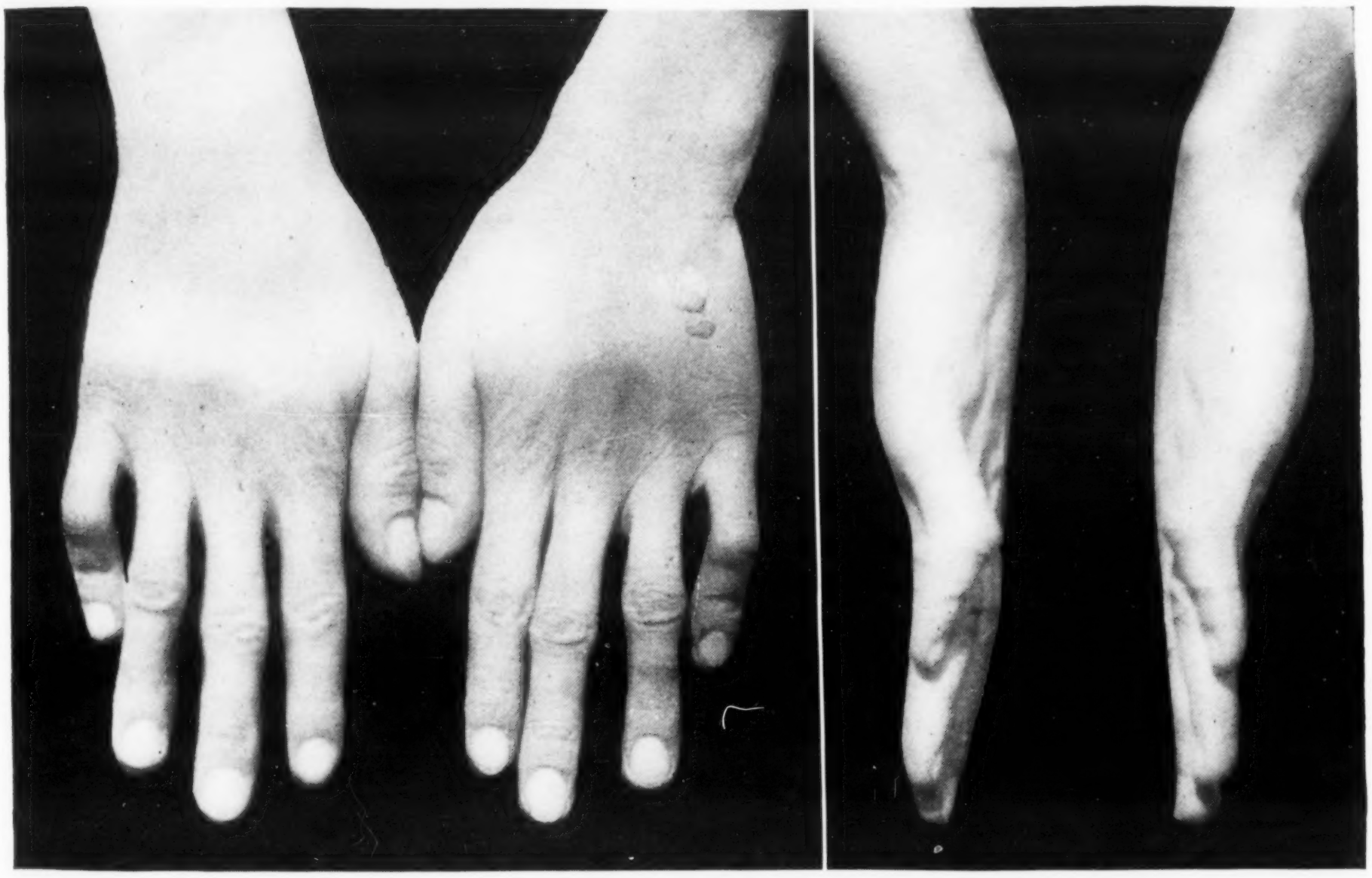
The condition may be described as a peculiar crooking of the little finger at the proximal joint when the other digits are straightened (Figures 3 and 5). The finger cannot be forcibly straightened, due to an apparent shortness of the tendons having their insertion in the region of this joint.

The x-ray photograph reveals a curved termination of the proximal phalanx of the affected finger (Figure 4). The medial phalanx is in prolongation with this curved portion, thus establishing the external bend or crook

X-RAYS OF THE BENT FINGERS

Figure 4

Part of the left hand and both little fingers are shown. The external appearance of these hands is shown in Figure 5. Note the unusually long and slender fingers, and that the tip of the first phalanx of both little fingers is bent.



TWO VIEWS OF THE BENT FINGERS

Figure 5

Whether the shortened tendons or the bent bones appeared first in development it is impossible to say. Although the mode of inheritance of this character has not been determined, it appears to be certainly hereditary, as in the one family reported it was passed on from father to son.

in the finger. The above title thus refers to this joint where, due to this curvature, the articulation is below the first phalanx rather than in direct prolongation.

The history of this trait is indefinite but is unquestionably of hereditary origin as shown by the brief record. The condition occurs in both hands of the individual previously mentioned (Figures 4 and 5), and in one hand of the father (Figure 3). Further record was not available and no cause for the abnormal fingers could be assigned.

The hands and fingers of both subjects are long and slender, suggesting the condition known as dolichodactyly.[1] The short tendons are apparently definitely associated with the abnormal joint and it is recognized that either condition might induce the other in the process of embryological development.

The application of a definite nomenclature to this condition awaits further report on its prevalence, mode of transmission, and specific nature.

[1]Osborn, H. S. *Origin and Evolution of Life*, p. 76.

SCENE OF THE COURTSHIP

Figure 6

The author observing the courtship of *Cardiacephala myrmex* on the heart-shaped leaves of a Piperaceous shrub on Barro Colorado Island. Photographed by Dr. David Fairchild.

COURTSHIP OF THE CALOBATAS

The Kelep Ant and the Courtship of Its Mimic, *Cardiacephala myrmex*

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THE observations recorded in the following paper were made at the tropical laboratory on Barro Colorado Island in the Panama Canal Zone, an institution concerning which my friend, Dr. David Fairchild, published a very interesting article in a recent number of the JOURNAL OF HEREDITY. He called attention to some of the larger opportunities which might attract serious students of animal and plant life to the station, but he could not, of course, descend to details. During the past summer Dr. Fairchild, his son, Mr. Graham Fairchild, Mr. Nathan Banks, Dr. Curt Richter, Mr. Frederick Burgess, Dr. George C. Wheeler and myself passed several delightful and profitable weeks on the island, where Mr. James Zetek, the custodian of the laboratory, and his assistant, Mr. I. Molino, ministered constantly to our comfort. To say that we were profoundly impressed by the opportunities for investigation afforded by the laboratory, is a mild statement. The incidental observations here recorded were made within a few hundred yards of the building and relate to the performances of a couple of insects selected from an inexhaustible fauna.

The Kelep

One of the insects is the large, rust-red "kelep" ant (*Ectatomma tuberculatum*), which twenty years ago was given a reputation by Mr. O. F. Cook, who observed its habits in Guatemala and conceived that it might be introduced into the Southern States for the purpose of destroying the cotton boll-weevil.[1]* The experiment failed and the insect has since been relegated to an undeserved oblivion — undeserved, because it is one of the commonest and most conspicuous ants in Tropical America. I have seen it almost daily in Panama, Guatemala, and British Guiana stalking sedately over the foliage of the bushes along the sun-flecked trails through the jungles or, more frequently, standing on some leaf, with its peculiarly wrinkled head uplifted and its long antennæ outstretched. At such times it presents the appearance of having been smitten suddenly by some brilliant idea, and recalls the ant-prophets in Arpad Ferenczy's recent satirical romance, *The Ants of Timothy Thummel*. But far from being an even ordinarily intelligent and enterprising insect, the kelep might be more aptly described as one of the most inveterate loafers and cowards of the ant world. It sometimes captures small feeble or moribund insects and carries them slowly to its nest, but more frequently it is seen feeding at the large saucer-shaped extrafloral nectaries of the various species of *Inga* which abound in the jungle. This fondness for nectar probably accounts very largely for its presence on cotton plants in Guatemala and elsewhere, since these are known to have well-developed extrafloral nectaries on their involucres.

The kelep makes its nest in the ground at the base of a small tree, but unlike the more blackish and equally common *Ectatomma ruidum*, which surrounds its nest with a flat earthen crater, *tuberculatum* constructs a singular tubular gallery, which runs straight

*For numbered references see *Literature Cited* at end of article.

THE KELEP'S FRONT ENTRYWAY

Figure 7

Entrance to nest of Kelep ant (*Ectatomma tuberculatum*) on Barro Colorado Island. The entrance is a tube of fibrous vegetable debris 2½ feet long by 1½ inches in circumference. Only the upper portion of the tube is shown in the photograph by Dr. David Fairchild.

A KELEP CAFETERIA

Figure 8

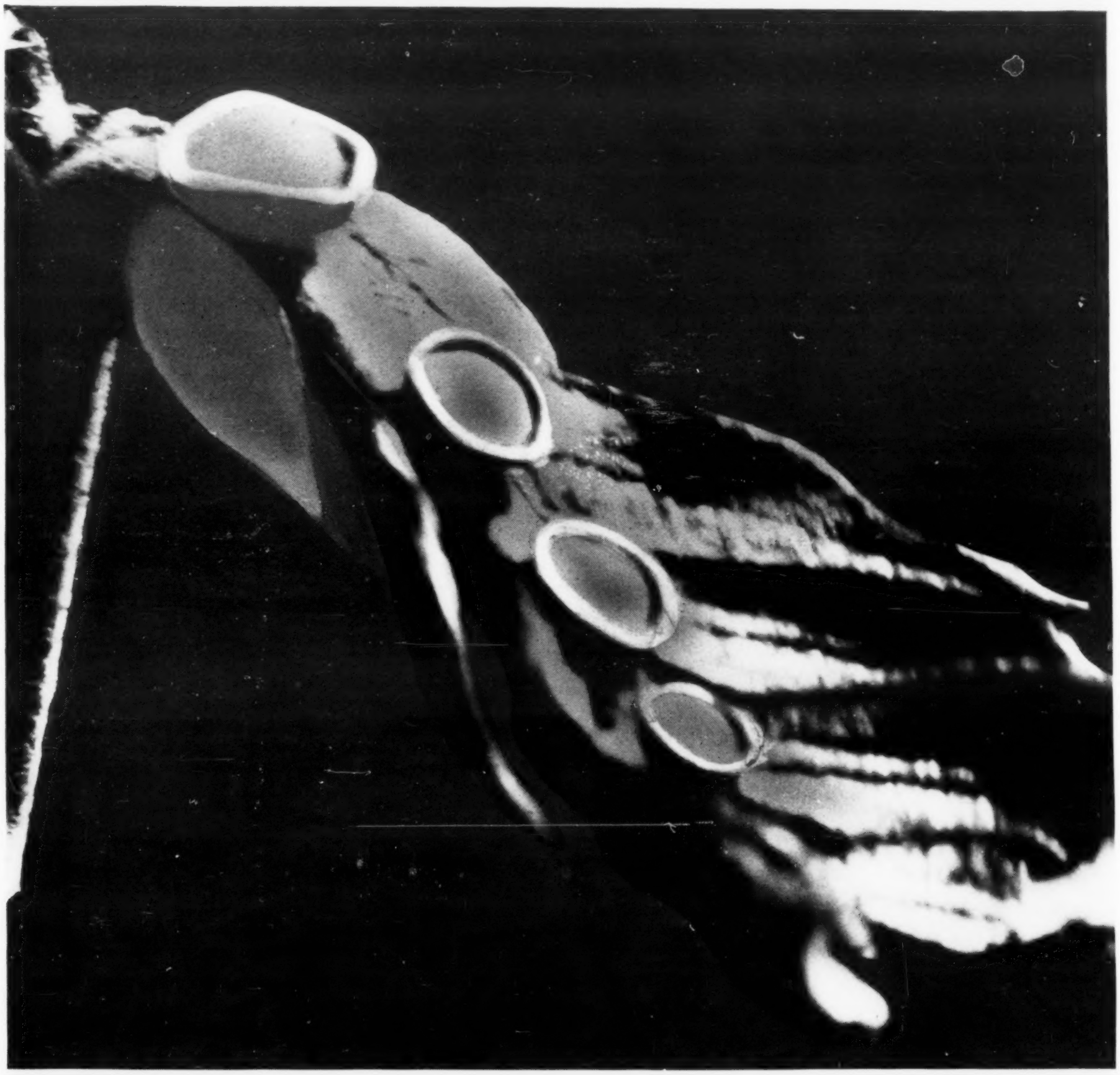
Young leaf of *Inga* sp. showing platter-shaped extrafloral nectaries. The cut leaf was left over night in a bottle of water and in the morning each nectary was full to overflowing with nectar. Photographed by Dr. David Fairchild.

up the bark of the tree to a height of two to three feet above the earthen entrance of which it is a continuation. This tube is nearly 1½ inches in diameter and consists of carefully felted, fibrous, vegetable detritus, as shown in Dr. Fairchild's excellent photograph of the upper end of a gallery. When the gallery is torn away from the tree the returning keleps often have some difficulty in finding the opening of their nest in the ground. It is strange that Cook, who saw the nests of this ant in Guatemala and described their earthen chambers (*loc. cit.* p. 6) failed to mention the felted gallery, which is not known to occur in any other species. That it is a constant feature is shown by the fact that it was always present, both in the nests on Barro Colorado Island and in those which I observed at Kartabo in British Guiana.

Cardicephala Myrmex

In company with the kelep, on the same plant and sometimes even on the same leaf, occurs a slender Micropezid fly, which, though somewhat smaller, is so similar when seen in the subdued light of the jungle that it would be described by many entomologists as a true mimic of the kelep. This fly, which Mr. C. W. Johnson has identified as *Cardiacephala myrmex* Schiner, measures 6-8 mm. in length and is ferruginous red, like the kelep, but the head and terminal abdominal segments are shining, iridescent blue. The short, narrow wings have two broad brown cross-bands, a narrower apical band and a blackish spot near the center. These markings are distinctly seen in Dr. Fairchild's photograph. The median and hind femora of the very long, slender legs are strongly thickened at the middle. While the insect is resting or running over the leaves the wings are compactly folded over one another on the back of the abdomen. The males and females are quite alike, except in their primary sexual characters, the latter having the tip of the abdomen long and tapering and folded forward under the venter, while the male genitalia have a similar position but are much smaller.

Reference to the literature shows that Schiner described *Cardiacephala myrmex* in 1868 from specimens collected by the "Novara" expedition somewhere in South America. Mr. Johnson has shown me specimens from Bartica, British Guiana, and Van der Wulp in

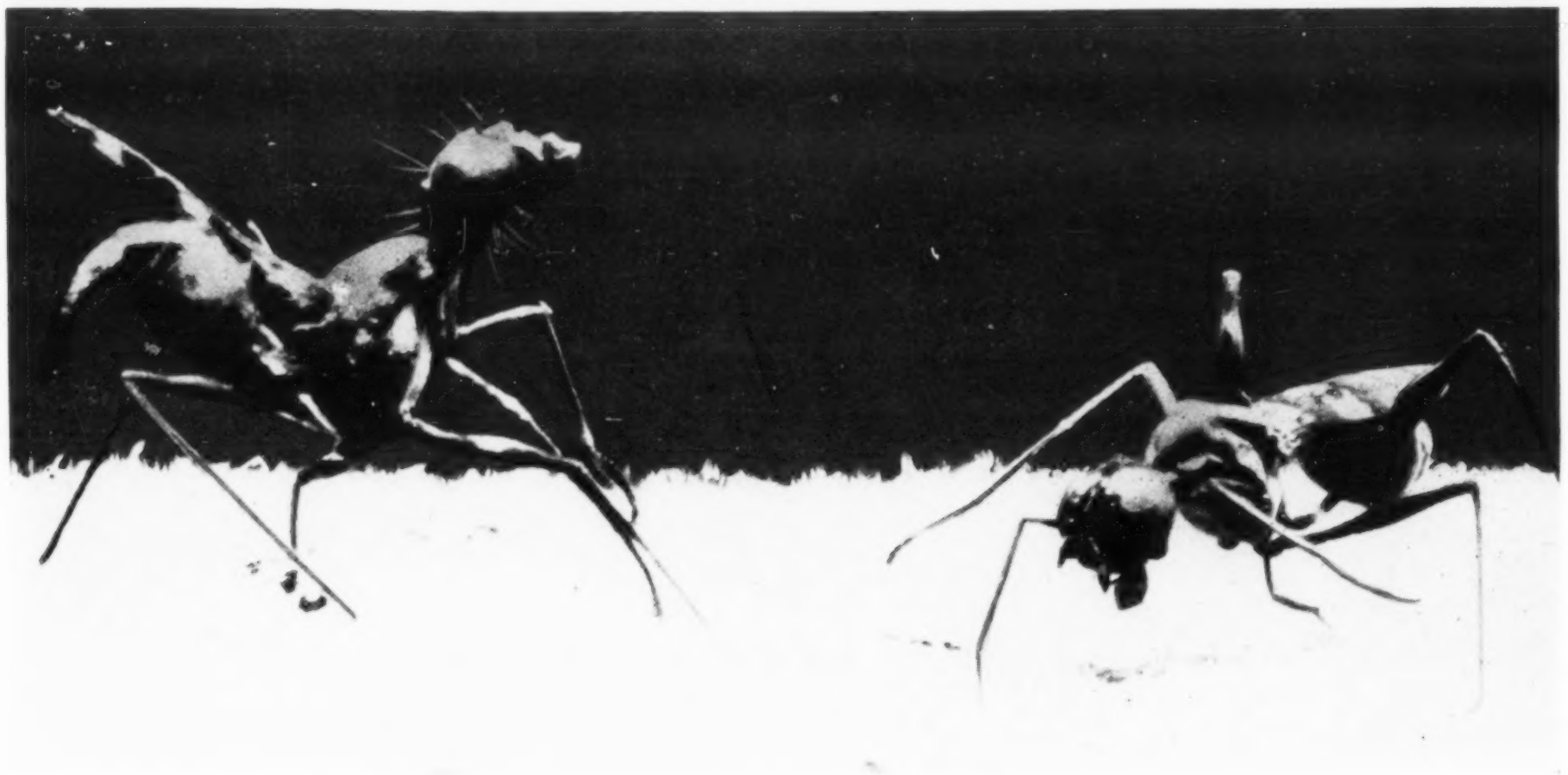


SAUCERS OF HONEY
Figure 9

Extrafloral nectaries of young and just unfolded leaf of *Inga* sp. under a magnification of 7½ diameter, to show how like saucers of honey these structures may appear to the small insects like the Kelep that visit them. Photographed by Dr. David Fairchild.

the "Biologia Centrali-Americana" records it from Vera Cruz and Tabasco, Mexico. It is therefore widely distributed in Tropical America. The specific name *myrmex* shows that Schiner was sufficiently impressed by the myrmecoid appearance of the dried specimens, but these are much less ant-like than the living individuals. Of course, the generic name, established by Macquart as far back as 1843, refers to the heart-shaped head, not to the insect's having its heart in its head, as we might infer from the amorous antics about to be described.

This behavior was first witnessed by Mr. Nathan Banks, but was later observed repeatedly by the other workers at the laboratory. During a period of at least two weeks the flies could be seen going through the performance on any sunny morning or afternoon. A dozen or more individuals of both sexes select and for many days use as a playground the large horizontal leaves of some bush growing along the edge of



COURTSHIP OF THE CALOBATAS

Figure 10

Male of the Micropezid fly, *Cardiacephala myrmex*, engaged in courting the female. The male is to the right and is in the act of swinging his abdomen to one side. The female is curving her body in an arc and beginning to throw back her head in anticipation of being fed by the male. Photograph 5 diameters, by Dr. David Fairchild.

the jungle trails. One bush, partly shown in the photograph, a vigorous Piperaceous plant, with large cordate leaves, was such a favorite resort which we visited again and again. The flies run about on the upper surfaces of the leaves with rather jerky movements or flit from one leaf to another. They evidently recognize one another by sight. The females are very coy and often drive the males away by making sudden lunges at them when they approach too closely. The males, too, occasionally fight with other males, rising perpendicularly on their long hind legs and facing one another as in the Javan Micropezid described in the sequel.

If carefully observed when alone, the male is sometimes seen to stand still and regurgitate from the tip of his proboscis a small drop of liquid, which he at once swallows, only to produce another drop and withdraw it in turn. This may be repeated several times and is obviously the same as the behavior described by Hewitt[2], Graham-Smith and Purvis[3] in the common housefly. In both cases the alimentary canal is distended with liquid and the indecent creatures amuse themselves by alternately regurgitating and swallowing portions of their food.

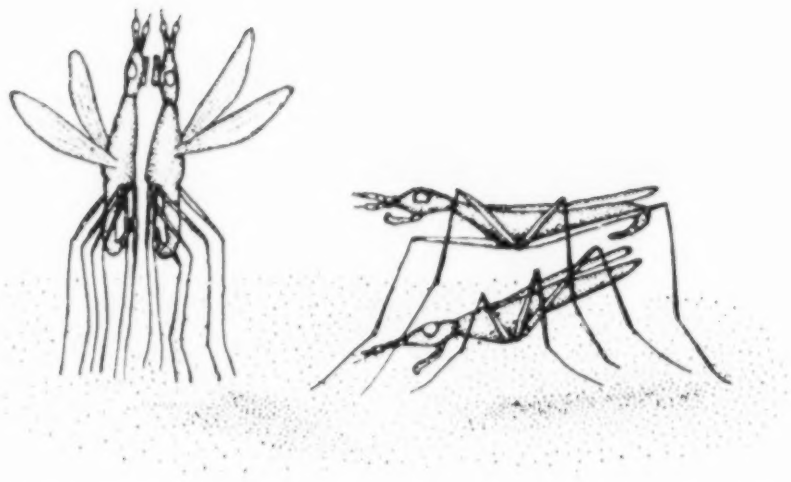
If the female *Cardiacephala* is willing to receive the male, he is permitted to approach within a few centimeters. Facing her he then performs a peculiar dance, stepping first to one side and then to the other, swaying his abdomen towards her and at the same time downward till it strikes the surface of the leaf. He may do this three or four times, one might perhaps conjecture with the purpose of enabling the female to estimate his *embonpoint*, or the amount of juice in his crop. Perhaps, however, he is merely displaying to its best advantage the beautifully iridescent surface of his terminal abdominal segments. At any rate, the female, after witnessing this *danse du ventre*, seems to indicate to the male by some very very subtle sign, which I have been unable to detect, that she is ready to receive his embrace. She instantly bends her body in an arc by throwing her head back and turning up the tip of her abdomen. The male is on top of

her at once and bringing his proboscis in contact with hers, places a drop of food on it and almost at the same instant inserts his intromittent organ into the tapering apex of her abdomen. The female quickly straightens her body and the pair now remain together, usually for as many as ten to fifteen minutes, the male with his fore tarsi parallel and planted on the sides of the female's prothorax and his other pairs of feet on the leaf. Occasionally he reaches forward with his fore tarsi and scratches the female's eyes, but more frequently he advances his head and proboscis and with a peculiar pecking movement places a minute drop of regurgitated liquid on the upper corner of one of her eyes. She at once reaches up with her forelegs, wipes off the droplet with her tarsi and draws them over her proboscis. These acts on the part of the male and female may be repeated a dozen or more times. In the meantime the couple may run about or stand still for short periods, the female determining the direction to be taken and the stops. Finally, with a sudden kick of her hind legs she dislodges the male and the couple separate. It is probable that the male is kicked off as soon as the female perceives that the supply of liquid food in his crop is exhausted. Sometimes a stray male may come up and dance before a female *in copula*, but usually the couple are left alone. After mating the female may in a short time accept another partner. When she does this she is, perhaps, actuated more by hunger than by lust.

Courtship of Other Flies

Although the courtship and mating of *Cardiacephala* are extraordinary, even stranger scenes will probably be witnessed by the observer who can devote his attention to the other Central American Micropezids. There are numerous species frequenting the leaves and tree trunks on Barro Colorado Island and I was able to see enough of their behavior to state that each seems to have its own peculiar type of courtship. This is indicated also by the only account of mating Micropezids that I have been able to find in the literature, a note by Jacobson on the Javanese *Nerius fuscus* Wied., hidden away in a taxonomic paper on East Indian Diptera by de Meijere:[4] I here translate the note and reproduce the accompanying sketch:

I captured the whole lot of 14 specimens together on a "kelor" tree (*Moringa pterygosperma*) in my garden. This tree, which is dying and shows many decayed spots in its trunk, had evidently been visited by a woodpecker that had hacked the bark to pieces in many places. On these spots, where the sap was trickling out, the flies had congregated to lick up the sap, to copulate and oviposit. I will here describe in more detail their peculiar behavior during copulation. Both females and males seem to vary considerably in size. The peculiar behavior consists in the manner in which the preferred males defend their females from rival males. As a rule, these flies run about high on their legs, so that there is a considerable space between their bodies and the bark. Now the males stand in such a position over the females that the latter are completely enclosed by their legs. The females then run with their bodies very close to the bark, that is, in a crouching posture. Whenever the female moves the male follows, usually covering the female with his body. Whenever another male comes too near the pair, the male covering the female makes a sudden sally, with the result that the rival usually at once flies away. All the movements of these flies are more or less jerky. But the rival male is not always ousted and then a very amusing contest ensues. The two males raise their bodies perpendicularly, spread their wings and set them in rapid vibration. Thus with their bodies pressed together they kept pushing one another, one of them often with his fore legs thrown over those of his opponent. The struggle, body to body, is usually of short duration, but I once observed a contest that lasted four minutes and during that period the rivals pushed one another alternately backward. After each sally the male returns to his female, but if he happens to be driven away, the female at once accepts his rival. While the pair are thus running about the bark, the female licks up the sap from its crevices, investigates all its depressions and fissures with her proboscis and if one of them seems suitable, thrusts her pointed abdomen into it and deposits an egg. Copulation occurs very frequently but only for brief periods. During its occurrence the female presses her head against the tree, so that the tip of her ab-



COURTSHIP OF EAST INDIAN FLIES

Figure 11

Courtship of a Javanese Micropezid fly, after E. Jacobson (from J. C. H. de Meijere). To the left two males fighting; to the right a male covering and protecting a female.

domen is raised. Copulation then ensues while the male is standing over her.

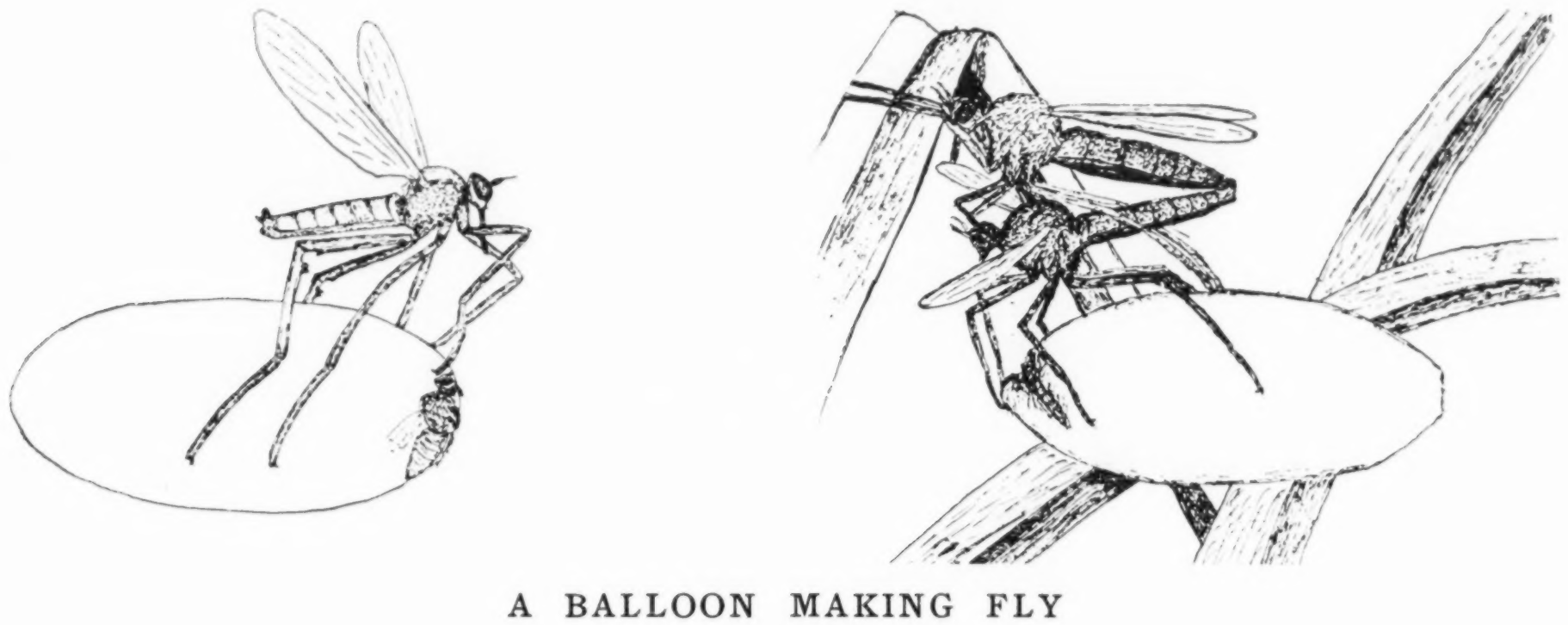
Types of Courtship

Now the above described nuptial performances of Micropezid flies, which live on the juices of plants, acquire a peculiar significance when we consider the even more astonishing behavior of the predaceous flies of the family Empididæ as revealed in a number of short papers by Osten Sacken, Becker, Mik, Girschner, Aldrich and Turley, Howlett, Hamm and Poulton.* The investigations of these authors enable us to arrange the species of Empididæ in the following groups which seem roughly to represent advancing steps in courtship:

(1) Both sexes capture prey (usually other small flies) and feed upon them. In this respect they resemble other predaceous, or robber flies, like the Asilidæ, a family from which the Empididæ may be descended. The species of *Tachydromia*, *Hybos* and a few *Empis* (*trigramma*, *punctata* and *scutellata*) belong to this group. Hamm (1908, p. 159) describes the rather simple courtship of *E. trigramma* as follows: "On June 5th at 6.48 P. M., I was looking at a female *trigramma* resting on an elder leaf, when a male alighted about an inch distant from her, fluttered his wings for a few seconds, then raised his anterior legs and waved them about. The female then fluttered her wings and raised her anterior legs and moved them about also, apparently in response. The male then rubbed the anterior tarsi together for some seconds, moving them quickly and at the same time rapidly vibrating his wings, which were maintained in a horizontal position. These actions were repeated with variations by one or the other for the space of three minutes. The pair had now drawn closer so that each was able to touch the other's anterior tarsi in a caressing manner. This they continually did, the male every now and then rapidly vibrating his wings. These actions continued for over two minutes, when the female slightly raised the apex of her abdomen, the male gently flew on her back, and pairing took place immediately. The total time occupied in courtship was,

*Although we have a great many species of Empididæ, Aldrich, Turley and Melander appear to be the only Americans who have written on their behavior; the remaining literature refers exclusively to European forms. As a possible aid to those who may wish to study our species I add the following list of the more important papers in chronological order:

Baron C. R. Osten Sacken, A singular Habit of Hilara. Ent. Month. Mag. (1) 14, 1877, p. 126; Becker, Hilara sartor n. sp. und ihr Schleier. Berlin Ent. Zeitschr. 1888, p. 7; J. Mik, Ueber ein spinnendes Dipteron, Sitzb. zool. bot. Ges Wien 1888, p. 97; E. Girschner, Zur Biologie von Hilara. Ent. Nachr. 1889, p. 220; Adam Handlirsch, Beitrag zur Kenntniss des Gespinstes von Hilara sartor Beck. Vehr. zool. bot. Ges. Wien 1889, p. 623; J. M. Aldrich and L. A. Turley, A Baloon-making Fly, Amer. Naturalist 33, 1899, p. 809-812, 3 figs.; J. Mik, Einige Worte uber Hilara sartor Beck., Ent. Nachr. 20, 1894, p. 49-53; E. Girschner, Beitrag zur Biologie von Hilara, *ibid.* 20, 1894, p. 61-64; J. Mik, Ein Beitrag zur Biologie einingen Dipteren II Ueber spinnende Hilaren, Wien. Ent. Zeitg. 13, 1894, p. 271-284, Pl. 2, Figs. 8-13; A. L. Melander, *Monograph* of the North American Empididæ. Trans. Amer. Ent. Soc. 28, 1902, p. 195-367, 5 pls.; M. Howlett, Note on the Coupling of Empis berealis. Ent. Month. Mag. (2) 18, 1907, p. 229-232; A. H. Hamm, Observations on Empis livida L., *ibid.* (2) 19, 1908, p. 181-184; A. H. Hamm, Further Observations on the Empinæ, *ibid.* (2) 20, 1909, p. 192-143; E. B. Poulton, Empidæ and their Prey in Relation to Courtship, *ibid* (2) 24, 1913, p. 177-180.



A BALLOON MAKING FLY
Figure 12

The males of certain species of *Empis* construct a hollow "cocoon" or "balloon," the purpose of which is to attract the female. She is given the "balloon" and toys with it during mating, afterwards dropping it. On the left is shown a male in flight with his balloon. Note the dead insect embedded in the front end of it. This is always present, and seems to serve as a stimulus to the construction of the balloon. From Aldritch and Turley, *Am. Nat.* 33: 810. 1898.

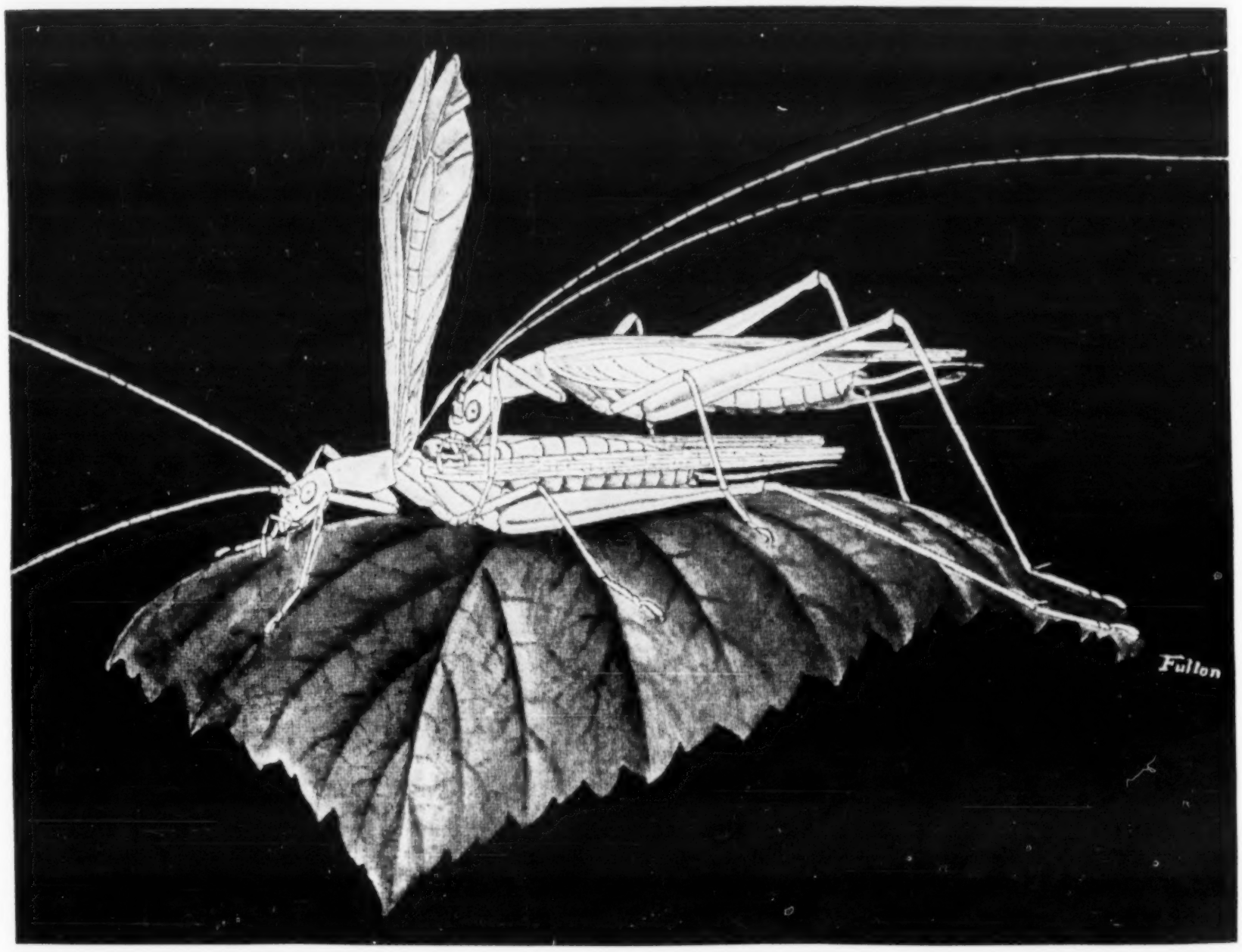
therefore, about five-and-a-half minutes."

(2) The male alone captures prey, bites and paralyzes but does not otherwise injure it, and flying up to the female, usually while she is dancing in the air with other females, presents it to her. Mating then takes place on some plant, while the female devours her bridal gift, piercing it in many places, kneading it and imbibing its juices. As soon as this is accomplished copulation ceases and the prey, now reduced to a crumpled mass, is dropped. This behavior was repeatedly observed by Howlett (1907) in *Empis borealis* and *Hilara maura* and by Hamm (1908, 1909) in *Empis opaca, tessellata* and *livida, Pachymeria femorata* and *Rhamphomyia sulcata.*

(3) In this group, represented by various species of Hilara, as Poulton (1913, p. 179) states, "the prey or object provided by the male is not devoured by the female, but becomes, as it were, an ornament or plaything providing some indispensable stimulus" to mating. He summarizes Hamm's unpublished observations as follows:

> All the species fly over water, and the prey or other object is always picked up from its surface by the male Hilara. The male takes floating insects of all kinds—sometimes specially Diptera, sometimes Aphids—scales off overhanging tress or other fragments of plants. Some of the species will accept almost any floating object, while others seem to restrict themselves to particular insects, such as Aphidæ. When the object is very heavy, the male, after seizing it, spins round with great velocity till the load rises on a cone of water, and is finally lifted from the apex. In Mr. Hamm's experiments, disabled Diptera of the genus *Chironomus*, etc., stamens of buttercups, and ray florets of daisies strewn on the water were soon taken by the males, and afterwards found in the possession of the females Pairing invariably occurs upon the wing, but numbers of specimens show that a sweep of the net through the swarm at first catches nothing but males carrying the objects that had been strewn on the water, while a later sweep catches pairs still carrying the same objects. * * * * Mr. Hamm's admirable experiments also enabled him to determine that the females carry the objects provided by the males; for although they are never retained when the pairs are captured, the white florets or the yellow stamens can be seen hanging from the lower Hilara of each flying pair, and the lower is invariably the female.

(4) In this group, represented by several species of Hilara, notably *H. maura, interstincta, acronctha* and *pruinosa*, according to Girschner (1899) and Mik (1894), and an American *Empis* (*E. acrobatica*), the male catches and kills a minute fly and envelops it in a veil or an ellipsoidal mass of white, frothy or silky substance, which is in all probability a product of his oral, or salivary glands. This object is



CARRYING HIS NECTARY WITH HIM

Figure 13

Female of Tree Cricket (*Oecanthus niveus*) feeding on the secretion of the metanotal gland of the male just before mating. (After B. B. Fulton).

given to the female as a bridal gift and is turned about in her feet while she is mating and then dropped. The most interesting account of these nuptial "balloons" or "cocoons" is by Aldrich and Turley (1899), but it appears that their statements may not be altogether accurate, since they describe the female as being on top *in copula* and the male as toying with the balloon. According to Poulton, in his review of Hamm's observations, "the cocoon is spun upon the wing, so that the method of its construction cannot be followed. Captured individuals are often found to have extruded a viscid globule—probably the material out of which the cocoon is spun. There can be little doubt that in these extreme cases it is the cocoon itself which acts as a stimulus to the female, although the minute and almost invisible object usually enclosed in it, but sometimes dropped, is the stimulus which incites the male to spin. Cocoons that have been dropped, probably after pairing, are constantly picked up and used over again by other males."

(5) Apparently the males of some Hilaras, like the species observed by Osten Sacken (1877) and *H. sartor*, observed by Becker (1888), Mik (1888, 1894) and Girschner (1889, 1894) produce a peculiar fish-scale-like silken plaque, without a minute insect as its nucleus, and present it to the female. The observations on these Empidids, however, are incomplete and seem to require reinterpretation in the light of Howlett's and Hamm's investigations.

Food and Sex Instincts

It will be seen from the foregoing account that in many flies the food and sex appetites are very intimately associated in the female, that she may even become parasitic on the male to the

extent of requiring him to feed her and that she may sometimes be satisfied with a substitute, or dummy in the form of some little inedible object that she can play with while mating. The case of *Cardiacephala myrmex* is very interesting because the male feeds the female with regurgitated food, either directly during courtship, or indirectly, by placing it on her head when during copulation he is in such a position as not to be able to reach her mouth with his proboscis. Authors have suggested that this association of the food and sex appetites may arise from the more general and urgent physiological need of the female for concentrated food with which to bring her ovarian eggs rapidly to maturity. We might, therefore, expect among certain insects, which as a class exhibit so many marvellous examples of the greatest economy and parsimony in the utilization of food, that the male would be called upon to provide the necessary pabulum.

We find cases like the ones I have been citing even among the Orthopteroid insects, a complex of orders as primitive in structure and many of their habits as the Diptera are specialized. Thus Hancock[5], Boldyrev[6], von Engelhardt[7], and Fulton[8], have shown that the male tree-crickets of the genus *Oecanthus*, both in the United States and Europe, have on the back of the thorax a large gland, the secretion of which is greedily devoured by the female before or after she receives the spermatophore, an act which in these insects takes the place of copulation. That the glandular secretion has a food value is indicated by Fulton's observation of a female Oecanthus nymph in the fifth instar feeding at the gland of a mature male.

Finally, in some other Orthopteroids like the Mantids (*Mantis religiosa* and *Stagmomantis carolina*), the nutritive meaning of the male to the female is clearly revealed, for both Fabre and the Rau's[9] have shown that he himself is actually devoured piece-meal by his spouse during or after copulation. I quote part of the passage in which Fabre describes the gruesome spectacle, because it is such a fine example of the master's style and because it makes us wonder what he might have written about *Cardiacephala*, had he been privileged to witness its courtship on Barro Colorado Island.[10]

> We are near the end of August. The male Mantis, a slender and elegant lover, judges the time to be propitious. He makes eyes at his powerful companion; he turns his head towards her; he bows his neck and raises his thorax. His little pointed face almost seems to wear an expression. For a long time he stands thus motionless, in contemplation of the desired one. The latter, as though indifferent, does not stir. Yet the lover has seized upon a sign of consent: a sign of which I do not know the secret. He approaches; suddenly he erects his wings, which are shaken with a convulsive tremor. This is his declaration. He throws himself timidly on the back of his corpulent companion; he clings to her desperately, and steadies himself. The prelude to the embrace is generally lengthy, and the embrace will sometimes last for five or six hours. Nothing worthy of note occurs during this time. Finally the two separate, but they are soon to be made one flesh in a much more intimate fashion. If the poor lover is loved by his mistress as the giver of fertility, she also loves him as the choicest game. During the day, or at latest on the morrow, he is seized by his companion, who first gnaws through the back of his neck, according to use and wont, and then methodically devours him, mouthful by mouthful, leaving only the wings. Here we have no case of jealousy, but simply a depraved taste. I had the curiosity to wonder how a second male would be received by a newly fecundated female. The result of my inquiry was scandalous. The Mantis in only too many cases is never seated with embraces and conjugal feasts. After a rest, of variable duration, whether the eggs have been laid or not, a second male is welcomed and devoured like the first. A third succeeds him, does his duty, and affords yet another meal. A fourth suffers a like fate. In the course of two weeks I have seen the same Mantis treat seven husbands in this fashion. She admitted all to her embraces, and all paid for the nuptial ecstasy with their lives.

Descending, in conclusion, still further in the scale of Arthropods in search of additional evidence of the close linkage of the food and sex appetites, I may call attention to the

male-destroying propensities of female spiders. Petrunkewitch,[11] however, claims that the old story that the female attacks and devours the male immediately after mating is very far from the truth, but his observations show that *before* mating the male represents merely so much food for the female and that after mating he is careful to get out of her way. He says:

> Courtship in spiders is naturally hazardous, since it is always doubtful whether the female will meet the male in a friendly way. In the case of the hunting spiders the male therefore as a rule, begins his courtship from a safe distance, beats rapidly on the ground with his anterior legs, rises on the hind legs or walks head downward—a different mode of courtship characterizing each species—but he never stops watching the female and takes to his heels at the first sign of danger. Cannibalism is only too common among spiders. A robust hungry female does not recognize her mate in the male unless she is sexually excited, looking on him only as prey; but when she has had sufficient food and is sexually excited, the latter condition depending largely upon the maturity of the eggs and the temperature of the atmosphere, then the male is allowed to approach.

The interesting account of Dugesiella which follows is too complicated for discussion in this article and shows that in the spiders we are really concerned with a type of mating behavior very different from that of insects.

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The History of Domesticated Animals

GRUNDZUEGE EINER STAMMESGESCHICHTE DER HAUSTIERE, by DR. OTTO ANTONIUS, Privatdozent at the University and High School of Bodenkultur, Vienna. Pp. 337, with 144 illustrations, price $1.50. Jena, Verlag von Gustav Fischer, 1924.

The attempt to ascertain the origin of domesticated animals has fascinated many students; but it is one that offers peculiar difficulties. Evidence must be sought from many different sources—history, paleontology, archæology, and philology, as well as several branches of zoology. In every field the uncertainties are more numerous than the certainties; hence, it is not surprising that there are differences of opinion on important points.

The work of Dr. Antonius is not only the most recent, but it is a careful and critical study that will commend itself even to those who do not accept all his conclusions. The author depends largely on zoological evidence, criticising effectively that derived from the other sciences above mentioned. He shows a thorough knowledge of the literature, but at the same time an

independent spirit that leads him to depend much on his own studies.

Few naturalists will fail to find something of interest in this richly illustrated book. Space will permit mention of only one item, and I select his discussion of the dogs of America. On the discovery of the New World, many of the Aborigines were found to have dogs, and mummies in the Inca region of South America fortunately make it possible to describe some of these dogs accurately. There were at least three forms, bearing some resemblance to the modern shepherd dog, dachshund, and bulldog, respectively. The first named is said to be similar to the most primitive forms of the Old World; indeed, T. Noack described specimens of this, which he thought were the same as *Canis paulstris* Ruet., the dog of the Swiss lake-dwellers. Dr. Antonius thinks it probable that the pre-Columbian Brazillians also had a gray hound.

There are then several highly specialized forms that show a marked paralellism to European varieties of the dog. Are these to be explained as the result of independent and parallel development, from some primitive American wolf; or is it to be supposed that after these European dogs had become specialized, they were brought to South America via Alaska, for instance? Either hypothesis has some interesting implications. The author wisely suspends judgment, remarking that there is room for further research. Here is a field that ought to tempt some American student.

P. P.

Reindeer in Alaska Increasing

Although only about 90 tons of reindeer meat were shipped from Alaska to this country in 1923, indications on July 1, 1924, were that there would soon be a rapid increase in the quantity shipped. In 1923 the entire number of reindeer in the Territory totaled about 241,000, according to estimates made in 66 herds. The increase in the number of reindeer in Alaska each year runs from 33 to 45 per cent of the total number of animals in the herd. This percentage can be raised by a better understanding of herd management on the part of the Eskimos and other owners, and better business methods in marketing the meat will result in a higher output. The Biological Survey of the United States Department of Agriculture conducts important investigational work in Alaska in the interests of the reindeer industry, including studies of diseases and parasites, feeding experiments to determine the nutritive values of different types of native forage, poison-plant problems, herd management, and breed improvement.

U. S. Department of Agriculture.

FREQUENCY OF MUTATIONS FOR CHLOROPHYLL-DEFICIENT SEEDLINGS IN MAIZE*

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THE COMPARATIVELY new method of breeding, by selection in self-fertilized lines in normally cross-pollinated crops such as maize, rye, timothy, and red clover, has two main purposes. One is to eliminate undesirable germ plasm and to make available desirable strains of known hereditary characters; the other is to use the better strains in producing first generation crosses or in rebuilding a variety. The recent literature in this field contains abundant evidence of the large number of abnormalities which may be isolated from such crops; in fact, it sometimes appears difficult, especially in maize, to secure vigorous selfed lines free from all abnormalities.

Lindstrom[4] made a review of studies of inheritance in maize. Of fifty-six factors which condition the development of known characters, all were recessive except the series for plant and seed color and the factor for tunicate ears. Because of their recessive nature many of the undesirable characters appear only infrequently in normal maize varieties.

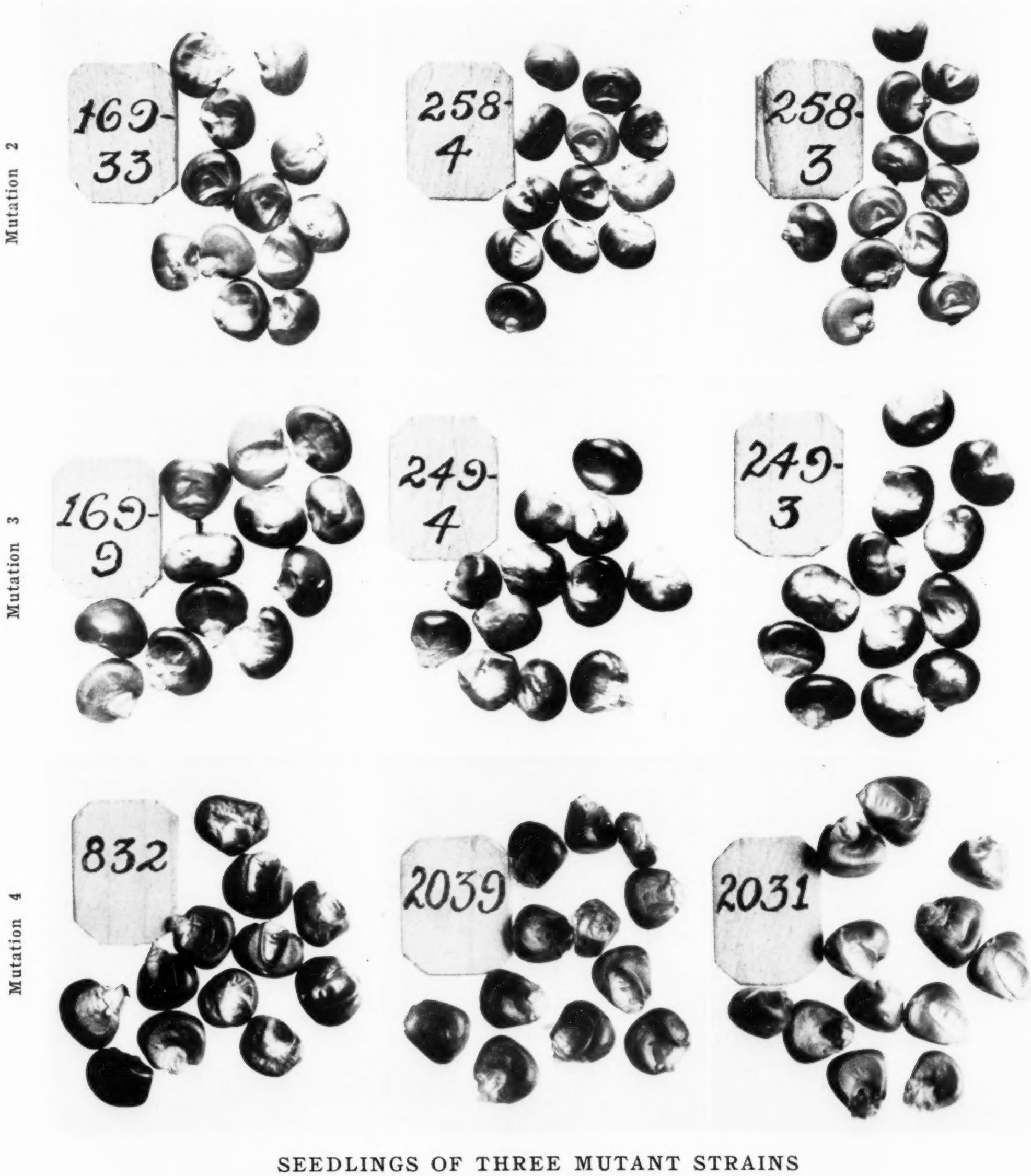
After a corn breeder has isolated vigorous selfed lines, free from abnormalities, he is at once confronted with the problem of keeping the strains pure. How often will mutations occur? And after having recombined the better strains to produce a new variety, will it still be necessary to continue selfing the parental strains or to again produce self-fertilized strains from the improved variety? In other words, will a new variety produced by this genetic mode of attack become again corrupted with abnormalities in a few years after it has been produced? There is comparatively little in the literature at the present time pertinent to this point, although there is some evidence which indicates that in certain cases mutations are relatively frequent.

Muller and Altenberg[6] reported gene mutations for lethal factors in the X chromosome of Drosophila. Twenty lethals occurred in 1,062 families or at the rate of 1 in 53. At the same time no mutations for other visible characters were recorded.

Zeleny[7] records the frequency of mutation for full, bar and ultra-bar eye in Drosophila. In full-eyed stocks no mutations to bar or ultra-bar eye were recorded in 46,290 flies. In 85,008 individuals with bar eye there were fifty-two separate mutations to full, or 1 in 1,636, which gives a mutation coefficient of 0.00061. In a total of 28,363 individuals in the bar eye series there were three known mutations to ultra-bar. In the ultra-bar group five mutations to full and three to bar were found in 8,681 flies; this gives mutation coefficients of 0.00058 and 0.00035, respectively.

As further evidence that the mutation rate varies considerably with the genetic factors concerned, Emerson[1,2] has recorded, in maize, a series of multiple allelomorphs for variegation in pericarp color. He reports that "some of the factors of this series have not

*Published with the approval of the Director as Paper No. 494 of the Journal Series of the Minnesota Agricultural Experiment Station.



SEEDLINGS OF THREE MUTANT STRAINS

Figure 14

The principal source of error in determining the frequency of mutation is the possibility that segregation may be caused by accidental crossing. In this event we would expect segregation on other characters, some of which would show as xenia. The uniformity of the seeds in the parent and progeny ears therefore indicates that cross pollination has not occurred.

Seedlings Grown from Parent Ear
Seedlings Grown from Progeny Ear which Segregated for Chlorophyll Deficient Seedlings
Seedlings Grown from Progeny Ear which Did Not Segregate for Chlorophyll Deficient Seedlings
Mutation 2
Mutation 3
Mutation 4

SEEDLINGS OF THE THREE STRAINS

Figure 15

Mutations 2 and 3 segregated, respectively, for white and white or pale luteus seedlings apparently devoid of chlorophyll. The virescent luteus seedlings of mutant 4 evidently contained some chlorophyll, but not enough to maintain the plants. These segregating ears appeared in a total of 953 strains of maize that had been self pollinated for from two to nine years without showing segregation for chlorophyll deficiencies. The appearance of aberrent seedlings in four of these lines seems to be due to mutation. The question of the frequency of mutations has practical importance for the plant breeder because if such germinal changes are of common occurrence, selected varieties will rapidly be corrupted with abnormalities, even if protected against outside contamination.

been observed to mutate, while others have mutated rarely and still others many times."

Muller[5] studied the manner of the origin of several mutations in the white-eyed series of Drosophila. He concluded that there was no evidence that mutations were more likely to occur in gametes or germ cells near the period of maturation that any other stage in the life cycle.

The relative frequency of occurrence of mutations for chlorophyll-deficiencies in maize seedlings apparently varies with the variety in question. It will be noted (see Table I) that the progeny of 39.4 per cent of all first-year selfed ears of Minnesota No. 13 segregated for chlorophyll-deficient seedlings. Of the other varieties studied the frequency of segregation for chlorophyll-deficiencies varied from fourteen per cent to as low as seven per cent. Since all of these characters are recessive and lethal, except perhaps certain virescents, natural selection would tend to decrease the frequency of their appearance in the normal variety. In this connection some work by N. Heribert-Nilsson[6] appears significant.

Nilsson reports a bloom-free ("wachsfreie") character in rye which acts as a simple recessive. Starting with a bulk plot of F_1 plants from a cross normal $\times$ bloom-free, growing the material in an isolated plot year after year, and eliminating the bloom-free plants before flowering time, he found that the appearance of bloom-free plants became less frequent in each succeeding generation. The results obtained fit very well the following formulæ:

N^2—1:1=phenotype ratio
N:1 =gametic ratio

when N= number of segregating generations; while the first and last terms of the ratio represent normal and bloom-free plants and gametes respectively. Thus, in the sixth segregating generation the gametic ratio of any pair of factors would be 6:1 and the phenotypic ratio 35:1.

While it is not possible to apply these formulæ directly to maize under field conditions, they do indicate very clearly that lethal characters such as white and yellow seedlings in maize will tend to become eliminated fairly rapidly. The fact that 39.4 per cent of the first year selfed strains of Minnesota No. 13 segregated for chlorophyll-deficiencies and that white seedlings occurred in the greater part of the segregating progenies indicates that mutations for a factor for white seedlings have occurred or are occurring fairly frequently in this variety. (See Table 1.)

Much of the data recorded in this article was taken in the regular corn breeding project at University Farm. A seedling test is made from the progeny of the selfed ears obtained. The method used is to test out all ears which contain at least 100 kernels by growing the progeny from each in about four inches of sand in the greenhouse during the winter. Twenty kernel samples are planted in rows and grown for approximately twenty days or until careful notes on germination and seedling abnormalities are taken. These data are summarized for the progenies of 1922 and 1923 selfed ears and for the F_1 to F_4 progenies of one cross (see Table II), these having been obtained from selfed strains which had not previously segregated for chlorophyll-deficient seedlings. A total of 953 lines varying from two to nine years selfed are recorded as having no seedling chlorophyll deficiencies. Four of the progenies of selfed ears in these lines segregated for seedling chlorophyll deficiencies (See Table 3). These are assumed to have appeared as a result of mutation. This gives a mutation rate of 1 in 238 or a mutation coefficient of 0.00422.

Photographs of seedling plants of mutations No. 2, No. 3, and No. 4 are shown in Figure 15. It was not possible to secure a photo of mutation No. 1. The white seedlings in mutations No. 1 and No. 2, and the white

TABLE I—The Frequency of Appearance of Chlorophyll Seedling Deficiencies in the First Year Selfed Strains of Minnesota Varieties of Maize.

Variety	Number of strains grown	Number of strains giving chlorophyll-deficient seedlings		Percentage of strains giving chlorophyll-deficient seedlings
Minn. No. 13	203	37 w 10 l 5 w, l 2 w, l, v 3 w, vw 12 vl 10 vw 1 w, l, vw	80	39.4
Rustler	36	2 w 1 l 1 vl	4	11
N. W. Dent	51	3 vw 1 l	4	7
	52	6 w 1 l	7	13
Longfellow	55	3 w 2 l 1 vl	6	11
King Phillip	44	6 w	6	14
Squaw	115	3 w 3 l 3 vw 4 vl 2 w, vl	15	13
Total	559		112	

w=white; l=luteus;
vl=viriscent luteus; vw=viriscent white.

TABLE II—Number of Progenies of Selfed Ears which Did Not Give Chlorophyll Deficient Seddlings.

Variety	No. of years selfed	Number of progenies	Total
Minn. No. 13.	2	62	
	3	61	
	4	25	
	5	9	
	8	18	
	9	3	178
Rustler	2	34	
	3	54	
	4	40	
	5	37	
	6	20	185
N. W. Dent	2	36	
	3	5	
	4	38	
	5	28	107
Minn. No. 23	2	51	
	4	5	56
Longfellow	2	61	
	4	15	
	5	13	89
King Phillip	2	31	
	4	118	
	5	17	163
Squaw	2	93	
	3	14	
	5	29	136
Cross 69-6 x 1-6	F_1 to F_4	39	39
Grand Total			953

TABLE III—Seedling Note for the Progeny of Parental Ear in Comparison with the Progenies of Later Generation.

	Variety	No.of years selfed	Ear No.	Relation	Seedling note*
Mutation No. 1	Minn.No.13	1	9-15	1922 parent line	151 N
	"	2	10-1	1923 progeny	39 N 5 w
	"	2	10-2	" "	143 N
Mutation No. 2	Squaw	1	169-33	1922 parent line	174 N
	"	2	258-1	1923 progeny	117 N
	"	2	258-2	" "	47 N
	"	2	258-3	" "	126 N
	"	2	258-4	" "	103 N, 28 w, 1 w stripe
Mutation No. 3	Squaw	1	169-9	1922 parent line	166 N
	"	2	249-1	1923 progeny	65 N
	"	2	249-2	" "	97 N, 38 w or pale 1
	"	2	249-3	" "	93 N
	"	2	249-4	" "	89 N, 24 w or pale 1
	"	2	249-5	" "	53 N
	"	2	249-6	" "	89 N
Mutation No. 4	69-6 x 1-6		811 x 1108	1919 cross	
	"		1600	1920 F_1	No abnormal seedl.
	"		500 to 800	1921 F_2	" " "
	"		500 to 900	1922 F_3	" " "
	"		832	1922 F_3 parent of 1923 progeny	147 N
	"		2009	1923 F_4 progeny	11 N
	"		2017	" " "	67 N
	"		2018	" " "	76 N
	"		2031	" " "	136 N
	"		2036	" " "	112 N
	"		2039	" " "	145 N, 61 vl (90% lethal in field

n=normal; w=white; l=luteus;
vl=viriscent luteus

or pale luteus seedlings in mutation No. 3 are apparently characteristic in being devoid of chlorophyll. The virescent luteus seedlings in mutation No. 4 contain some chlorophyll but they appear to be nearly, if not altogether, lethal under field conditions.

For mutations No. 1 to 3 inclusive it is apparent that while the parent lines gave only normal seedlings in 1922 that a part of the 1923 progenies, produced from seed of self-pollinated 1922 plants, were segregating for chlorophyll-deficiencies. The 1922 parent plant must then have been heterozygous. Mutation may have occurred in either the pollen mother cell or the megaspore mother cell in the parent plant in 1921, or mutation of a normal chlorophyll factor may have occurred in the germ tract prior to the production of the male and female reproductive cells of the 1922 plant which was self-pollinated. Mutation No. 4, which appeared in the F_3 generation of the cross, may be explained in a similar manner.

The possibility of error must be admitted for work of this nature. Every effort has been made to check up on the strains which have appeared to mutate. The parent seed agrees with the progeny seed for seed characters (as is shown in Figure 14). A recent greenhouse seedling test agrees with previous tests. There is, however, one other possibility for error which cannot be checked. It is the possibility of foreign pollen grains carrying the recessive factor for w, l or v having fertilized ovules on the 1921 ears in the selfed lines and the 1922 F_3 ear in the cross, thus resulting in these aberrant types. The uniformity of seed size of different generations in the various lines leads one to believe that this is not the correct explanation.

Conclusions

The frequency of the appearance of chlorophyll-deficiencies has been observed in first year self-fertilized lines of six varieties of maize commonly grown in Minnesota. The percentages of first year self-fertilized lines which segregated for chlorophyll-deficiencies varied from 39.4 per cent in Minnesota No. 13 to seven per cent in Northwestern Dent. The large percentage of segregating lines in Minnesota No. 13 indicates that recent mutations for chlorophyll deficiencies have occurred.

Four probable mutations for seedling chlorophyll-deficiencies have appeared in 953 selfed lines of maize which were obtained from seven varieties and the progeny of one cross.

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